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Systematic Position of Three European Heterobranch Gastropods

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Abstract. The external morphology of the soft parts, the shell, and the radula are described for the two Mediterranean gastropod species *Oxystele depressa* Granata (formerly in the Skeneidae) and *Skenea pellucida* Monterosato (formerly in the Skeneopsidae). *Oxystele depressa* is transferred to *Tomura* Pilsbry & McGinty, 1946 (Cornirostridae). *Skenea pellucida* is made the type of ***Xenoskenea*** Warén & Gofas, gen. nov., and classified in the family Hyalogryinidae, a heterobranch family with rhipidoglossate radula. ***Noerrevangia fragilis*** Warén & Schander, gen. et sp. nov. (Cornirostridae) is described from shallow water around the Faeroe Islands.

INTRODUCTION

Small, globular or low spired, "skeneimorph" and "vitrinellid-like" gastropods have for many years presented great problems for authors trying to classify them (Mediterranean species reviewed by GHISOTTI, 1984). The species have frequently been transferred between genera like *Skenea, Daronia, Cyclostrema, Skeneopsis, Tubiola, Vitrinella, Teinostoma,* and others. WARÉN (1992) attempted to stabilize the classification of some of the European species, mainly those belonging to the "Archaeogastropoda." This paper deals with three additional species belonging to the Heterobranchia.

Examination of living specimens of *Oxystele depressa* Granata and *Skenea pellucida* Monterosato showed that these species cannot belong to the families or genera where they previously were classified (Skeneidae and Skeneopsidae; SABELLI *et al.*, 1990), but have to be classified in two recently established families, Cornirostridae Ponder, 1990b, and Hyalogyrinidae Warén & Bouchet, 1992.

Noerrevangia fragilis gen. et sp. nov. (described herein) was found by Schander during field work at the Faeroe Islands. From the external morphology of the soft parts and from radular morphology this species fits well in the Cornirostridae.

The Cornirostridae and Hyalogyrinidae, in which these species are included, are not very well known to most malacologists, and the Heterobranchia, where they are classified, has been considerably enlarged during the last three years by the addition of a number of new families (listed herein, see "Systematics"). We therefore give a short supplement to the discussion by PONDER (1991) on this group.

MATERIALS AND METHODS

This paper is partly based on observations made on live specimens of *Oxystele depressa* and *Skenea pellucida* during field work. Color drawings were prepared and notes were based on weakly anesthetized specimens observed under a

stereomicroscope with a drawing tube. The observations are supplemented by the examination of shells from various collections. *Noerrevangia fragilis* was obtained in sediment residues fixed in formalin during field work in the Faeroe Islands, and it was not possible to examine the specimen alive. The soft parts were therefore extracted, stained with carm-alum, and examined under a stereomicroscope. Afterwards they were critical point dried and examined with scanning microscopy. Subsequently the soft parts were rehydrated and the radula extracted by dissolving the tissues in KOH.

The material we have had access to is listed under each species, with the location of the material: BMNH—Natural History Museum, London; MNHN—Muséum National d'Histoire Naturelle, Paris; SMNH—Swedish Museum of Natural History, Stockholm; USNM—United States National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Subclass Heterobranchia

PONDER (1991) discussed the following superfamilies and families as being of importance for the understanding of early heterobranch phylogeny:

Valvatoidea: Valvatidae, Orbitestellidae, Cornirostridae (see PONDER, 1990a, b, 1991; HEALY, 1990)
Architectonicoidea: Architectonicidae, Mathilididae
Pyramidelloidea: Pyramidellidae, Amathinidae
Omalogyroidea: Omalogyridae
Rissoelloidea: Rissoellidae
Glacidorboidea: Glacidorbidae (PONDER, 1986).

Four families have afterwards been added to the early heterobranchs:

Provalvatidae Bandel, 1991 (Valvatoidea; fossil, Jurassic)
Hyalogyrinidae Warén & Bouchet, 1992 (superfamily uncertain)
Tjaernoeidae Warén, 1991 (superfamily uncertain)
Xylodisculidae Warén, 1992 (superfamily uncertain).

New heterobranch families based on the genera *Ebala* Gray, 1847 (Pyramidelloidea) and *Cima* Chaster, 1897 (unknown superfamily) are in the process of being described (Warén, unpublished).

PONDER & WARÉN (1988) and PONDER (1991) favored an opinion that the Heterobranchia and Caenogastropoda were independently derived from different "archaeogastropod" groups and that the archiotaenioglossates represent an early offshoot of the branch leading to the caenogastropods. The recognition of the family Hyalogyrinidae (WARÉN & BOUCHET, 1992), with many heterobranch characters (Haszprunar, in preparation) and a rhipidoglossate radula strongly supports Ponder's view, rather than the scenario proposed by HASZPRUNAR (1988), who considered the heterobranchs and caenogastropods to be derived from a common ancestor, above the archaeogastropod level.

The detailed relations between the families listed above and the "subclasses" Pulmonata and Opisthobranchia are still incompletely known.

At present the most important task for increasing the knowledge about the lower heterobranchs is to extract, from the muddle of small "archaeo-" and caenogastropods, the right candidates for further exploration of the "missing links" between, on one side the "archaeo-" and caenogastropods, and on the other side between the "archaeogastropods" and the heterobranchs.

Family CORNIROSTRIDAE Ponder, 1990

Remarks: The family Cornirostridae was erected by PONDER (1990b) for the genera *Cornirostra* and *Tomura,* which are characterized by the following synapomorphies (in addition to a number of anatomical characters, which have not been examined in the species discussed herein and therefore cannot be evaluated):

—a bifurcate snout
—an anteriorly bifurcate foot
—a posteriorly bifurcate foot
—a single right pallial tentacle
—a bipectinate, basally attached ctenidium
—a hermaphroditic reproductive system with cephalic penis
—production of gelatinous egg masses
—a central radular tooth with highly developed lateral supports
—two or three partly overlapping lateral teeth.

The species of Cornirostridae are astonishingly similar to species of Vitrinellidae in their shell characters. Some species, for example *Tomura depressa,* can be recognized as belonging to the Heterobranchia by their heterostrophic larval shell, but an examination of the radula is usually needed to confirm the familial position.

Ponder interpreted the radula of *Cornirostra* to be taenioglossate, but we consider PONDER's (1990b:534, 543) "accessory plate" to be a third lateral tooth (PONDER, 1990b:figs. 4A, E).

In the same way it can be seen from PONDER's (1990b) fig. 3A of *Tomura bicaudata* Pilsbry & McGinty, that each row consists of nine teeth. The two lateral teeth are stuck together, but in fig. 3D, the outer lateral tooth has been bent towards the marginal tooth (to the right). In our Figure 9 this is more obvious, since the serrated lateral margin of the inner lateral tooth can be distinguished.

We therefore assume that *Cornirostra* and *Tomura bicaudata* have nine teeth per transverse row. Ponder (personal communication) has agreed with this interpretation.

It can also be seen from PONDER's (1990b) fig. 4D and E of *Cornirostra* that it is only the most lateral tooth which folds laterally when the radula is "opened." This is also our experience from *Tomura depressa* (Figures 7, 10). (In

T. bicaudata the two outer teeth fold laterally.) In a taenioglossate radula this unfolding takes place between the second and third tooth, and the two marginal teeth will be folded laterally. Consequently the radular formula of *Cornirostra* should be 1·3·1·3·1 and that of *Tomura* (*bicaudata*) 2·2·1·2·2 or (*depressa*) 1·2·1·2·1.

In the Orbitestellidae the transverse rows of teeth consist of five teeth (PONDER, 1990a). We can therefore not agree that these radulae are taenioglossate. This does not, however, disturb the relations between the Cornirostridae and the Valvatidae, because the presence of a rhipidoglossate radula in ***Xenoskenea***, *Hyalogyra*, and *Hyalogyrina* suggests the presence of such a radula in the early heterobranchs and that the taenioglossate condition of the valvatid radula is not homologous to that of the Caenogastropoda, although the radulae have the same number of teeth.

Noerrevangia fragilis also has the formula 2·2·1·2·2. Such a radula, as well as that of *Cornirostra* and *Tomura*, may have evolved from a rhipidoglossate-like radula similar to that of the Hyalogyrinidae.

Tomura Pilsbry & McGinty, 1946

Tomura PILSBRY & MCGINTY, 1946:15. Type species, by monotypy *Virtrinella* (*Tomura*) *bicaudata* Pilsbry & McGinty, 1946 (Florida).

Remarks: The crawling animal and the shell of the type species were figured by PILSBRY & MCGINTY (1945:pl. 2, fig. 9) and described in some detail by PONDER (1990b), based on topotypic material.

Tomura depressa differs from the type species in having one tooth less in the marginal field and by having a shell with an umbilicus. This will probably turn out to be of generic value, but since at present these two species are more similar to each other than to any other known species, we prefer not to introduce additional generic names before we can see a need for it.

Tomura depressa (Granata, 1877)

(Figures 1–11)

Oxystele depressa GRANATA, 1877a:146; GRANATA, 1877b:9.
Tharsiella tinostomoides FEKIH & GOUGEROT, 1977:224.

Type material: *Oxystele depressa*, not known; *Tharsiella tinostomoides*, holotype and 1 paratype from the type locality, 5 paratypes from Tunisia, Porto Farina, in MNHN.

Type localities: *Oxystele depressa*, Sicily, Strait of Messina, 65 m; *Tharsiella tinostomoides*, Gulf of Tunis, Khéreddinne.

Material examined: TUNISIA: Golfe de Gabés: NW of Mer de Bou Grara, diving, 10–15 m, 150 shells (MNHN); Canal d'Ajim, diving 10–32 m, 10 shells, 2 specimens (SMNH); Djerba, SE of El Kantara, 4–5 m, 3 shells (MNHN); Sfax, 3 shells, *leg.* Gougerot (MNHN); Gulf of Tunis, Porto Farina, 20 shells, *leg.* Gougerot (MNHN).

FRANCE: Corsica, Baie de Calvi, algal washing, 10–40 m, 2 shells (SMNH); Marseille, off Mejean, 37 m, 2 shells (MNHN).

ITALY: Livorno, off Capraia, 180 m, coll. F. Giusti, 1 shell; Sicily, Catania, Acitrezza, shell gravel, 36 m, 3 shells (SMNH); Sicily, Bay of Brucoli, 17 m, 1 specimen (MNHN).

SPAIN: Málaga, dredged in 20–40 m, 2 shells (MNHN).

Distribution: Throughout the Mediterranean and Rabat (Atlantic Morocco), usually in 10–50 m (OLIVERIO, 1982, 1985, 1988; our material). Shells commonly found, live-taken specimens rare.

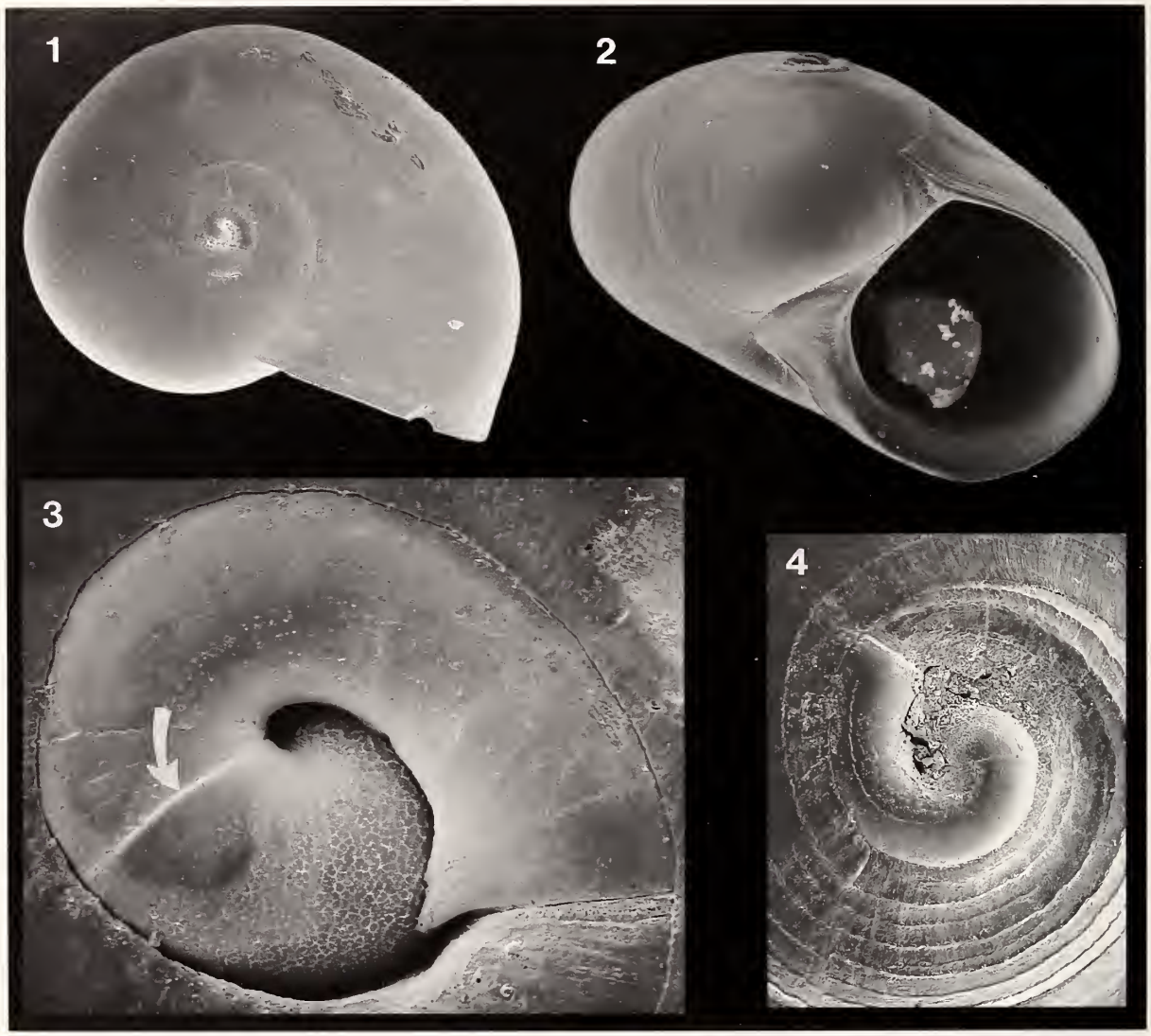
Redescription: The shell (Figures 1, 2) is very small, *Natica*-like, with an umbilical callus, transparent and rather solid. The larval shell (Figure 3) is hyperstrophic, diameter 150–175 μm. Protoconch I is only partly visible, and is mainly sculptured by a system of branching and anastomosing small ridges, except close to the demarcation to protoconch II. Protoconch II is almost smooth with only a few incremental lines and spirally arranged granulae, and consists of about 0.7 whorl. The teleoconch consists of about 2.0 whorls, usually almost perfectly smooth, separated by a very indistinct and shallow suture. Occasional specimens differ in having the initial part of the teleoconch equipped with a few spiral ridges (Figure 4), but this character varies in strength. The aperture is prosocline, almost tangential with the inner lip spread out to form a solid parietal and umbilical callus.

Dimensions: Maximum diameter 1.6 mm.

Operculum (Figure 11): It is thin and transparent, multispiral with short growth zone and central nucleus.

Radula (Figures 7–10): Formula 1·2·1·2·1. The radula is rather short and broad with about 20 transverse rows. The marginal tooth is broad and flat, roughly rectangular, with the distal end slightly obliquely truncated and denticulate. The outer, distal corner is slightly drawn out and cusplike, and the outer side of the tooth is finely denticulate almost to its base. The outer lateral tooth is short, rounded with the inner corner somewhat drawn out. This tooth is denticulate along its outer and apical sides. The inner lateral tooth is broad, apically evenly rounded and finely denticulate all around. The central tooth has a pair of lateral, wing-shaped supports and a central, distinct supporting ridge. The triangular cutting edge is serrated with about 9–11 denticles on each side of a central cusp. When tilted backwards, the distinctive anterior furrow becomes more obvious.

Soft parts (Figures 5, 6): The animal is almost colorless except for the pale brownish digestive gland and milky white cells in the anterior pedal gland. A small, bright yellow pigmented mantle organ is visible, dorsally and immediately behind the gill, through the shell. The foot is large, broad, thin, anteriorly expanded with drawn-out corners and is shallowly bifurcate; the sides are otherwise parallel; posteriorly it has a deep U-shaped notch, giving the posterior end a bifid appearance. The propodium is



Explanation of Figures 1 to 4

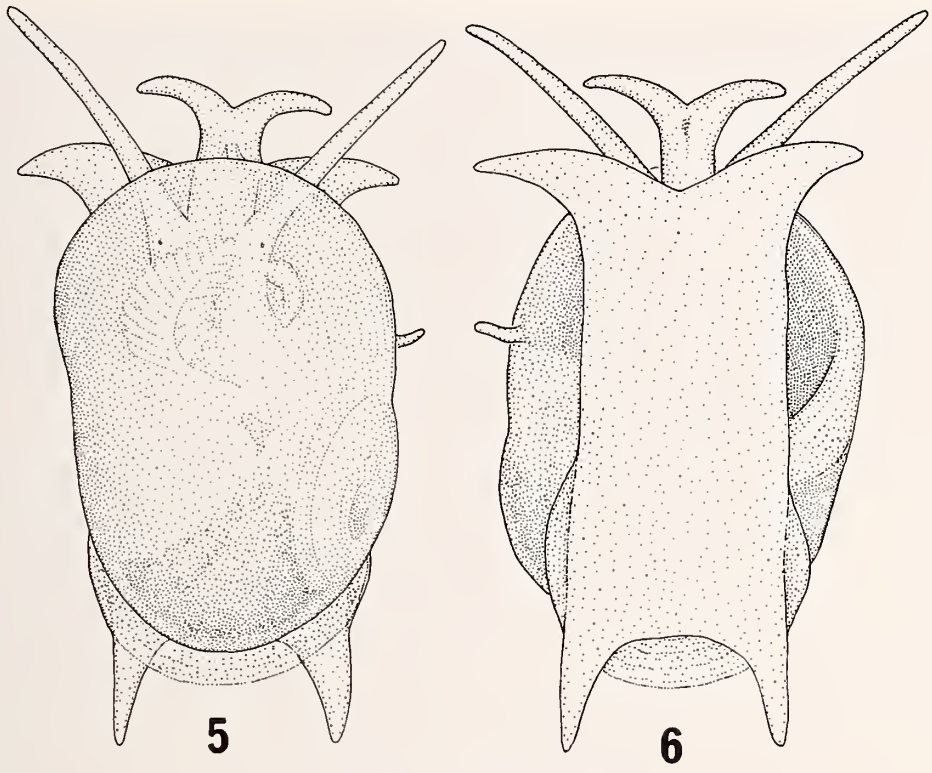
Figures 1–4. *Tomura depressa,* Canal d'Ajim, between Djerba and mainland, Tunisia. Figure 1. Apical view, 1.25 mm. Figure 2. Front view, 1.36 mm. Figure 3. Larval shell, diameter 171 μm. The arrow indicates the demarcation of protoconch I and II. Figure 4. Unusually strongly sculptured specimen, diameter of larval shell 152 μm.

not demarcated from the mesopodium; the metapodium (opercular lobe) forms a thin fold between the operculum and the mesopodium, hanging free between the two "tails." The head is small and slender, with long, cylindrical tentacles; the eyes are very small and deeply buried in the tentacle bases. A small, elongate, slightly tapering penis is attached laterally just to the right of the right cephalic tentacle. The snout is long and cylindrical, distally deeply bifurcate; a pair of jaws can be seen through the transparent central part of the snout. A minute pallial tentacle is present at the right corner of the pallial margin. The ctenidium is triangular, bipectinate, and attached basally.

Remarks: OLIVERIO (1982, 1985, 1988) reviewed the Mediterranean species *Tharsiella romettensis* (Granata) and *T. depressa* (Granata), their nomenclatorial history, and their distribution, but kept them both in *Tharsiella,* classified in the Skeneidae. For comments on *Tharsiella,* which is a junior synonym of *Cirsonella* Angas, 1877 (provisionally in Skeneidae) and *T. romettensis,* see WARÉN (1992).

Our description of the soft parts is based on two specimens observed alive. One, examined in the Golfe de Gabes, Tunisia, was taken on a sandy bottom in Canal d'Ajim, between Jerba and the mainland. The second specimen was taken on a sandy bottom off Brucoli in eastern Sicily, at 17 m depth. The rarity of live specimens is probably because the precise habitat is still unknown.

The external morphology of the head-foot of *Tomura depressa* agrees well with that of the type species of *Tomura* (*cf.* Figures 5, 6 with PONDER 1990b:fig. 2), but the shell



Explanation of Figures 5 and 6

Figures 5, 6. *Tomura depressa,* crawling animal. Sicily, off Brucoli, 17 m depth. Penis, jaws, eyes, and ctenidium visible through transparent tissues.

differs from *T. bicaudata* in lacking the umbilicus, which in *T. depressa* is filled out by a callus. PONDER (1990b) did not, however, find a pigmented mantle organ in *T. bicaudata* and the pallial tentacle is shorter in *T. depressa.*

The shell of *Tomura depressa* has the appearance of a miniaturized *Natica* with an umbilical callus, but examination of the larva shell shows that the initial whorl is very small, tilted, and depressed. Furthermore, the diameter of the protoconch is less than 0.2 mm, whereas the larval shell of European species of Naticidae with an umbilical callus has a diameter of about 1 mm or larger—*i.e.,* comparable to the size of an adult *T. depressa.*

Noerrevangia Warén & Schander, gen. nov.

Type species: ***Noerrevangia fragilis*** Warén & Schander, sp. nov.

Diagnosis: Small, *Vitrinella*-like cornirostrids with a paucispiral protoconch of half a whorl, and radular formula 2·2·1·2·2. Penis exceptionally large, equipped with open seminal gutter (Figure 19).

Description: See specific description of ***Noerrevangia fragilis.***

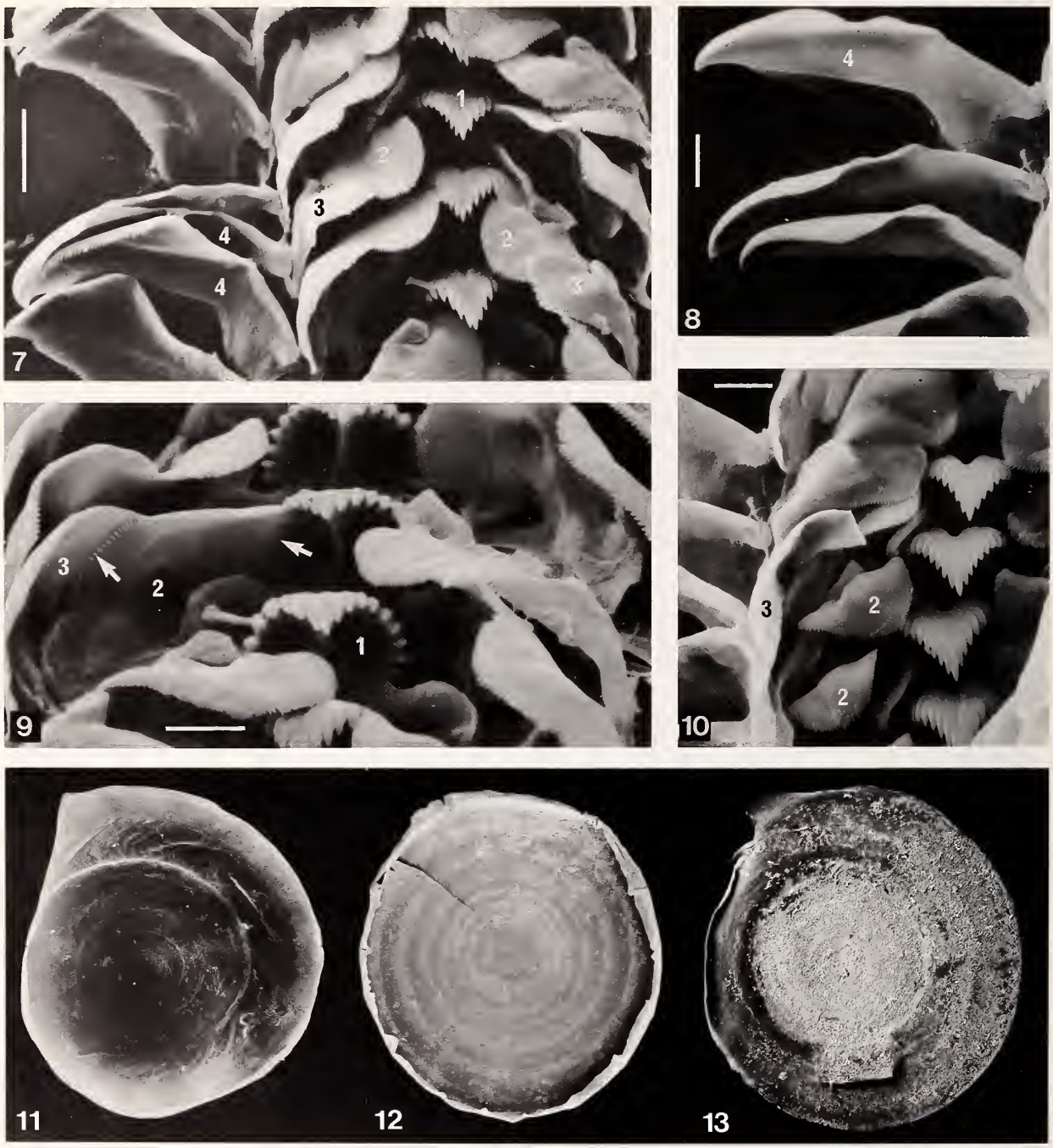
Etymology: Named after Professor Arne Nörrevang, director of the Kaldbak Marine Laboratory at the Faeroe Islands.

Remarks: The systematic position of ***Noerrevangia*** is not obvious from the shell. The anteriorly and posteriorly divided foot, the bifurcate snout, and the radular morphology do, however, indicate relations with the Cornirostridae. Additional similarities, although less diagnostic, are the right pallial tentacle, the presence of a cephalic penis, the bipectinate ctenidium, and the shape of the shell.

The shell and the head-foot of ***Noerrevangia*** closely resemble those of *Cornirostra,* but the spire of ***Noerrevangia*** is much more depressed and the penis of ***Noerrevangia*** has an open seminal gutter (internal in *Cornirostra*). We have therefore introduced a new genus.

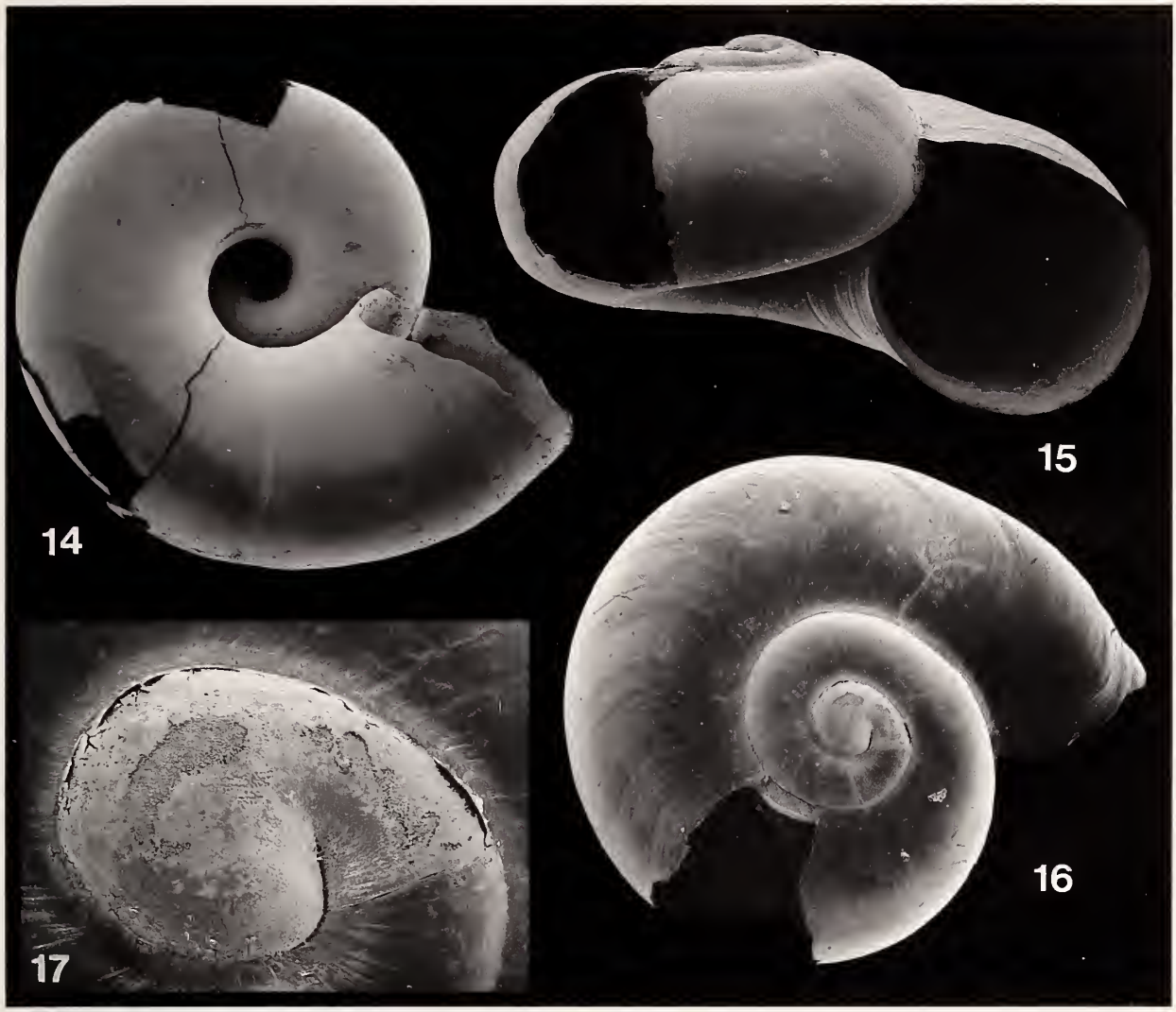
The radulae of *Tomura* and *Cornirostra* differ from that of ***Noerrevangia*** in the number of the marginal teeth (two in ***Noerrevangia***, one or two in *Tomura,* and one in *Cornirostra*), the number of lateral teeth (two in ***Noerrevangia***, three in *Cornirostra,* two in *Tomura*), and the shape of the inner lateral tooth, which has two main cusps in ***Noerrevangia***. (The two cusps of the first lateral tooth of ***N. fragilis*** may, however, be the result of fusion of two teeth.) The central tooth of the three genera shows great similarity in the development of the winglike lateral processes.

The protoconch of ***Noerrevangia*** is not similar to that of the other cornirostrids, but since there is no trace of a protoconch II, the development can be assumed to be lecithotrophic. In connection with a change from plankto-



Explanation of Figures 7 to 13

Figures 7–13. Radulae and opercula. Figures 7–11. *Tomura depressa,* Canal d'Ajim, between Djerba and the mainland, Tunisia. Arrows indicate indistinct borders between teeth; numbers indicate the sequence of the teeth, with the central tooth as number one. Figure 7. Vertical view. Scale line 10 μm. Figure 8. Another view of marginal teeth. Scale line 10 μm. Figure 9. Posterior view of central and lateral teeth. Scale line 5 μm. Figure 10. Vertical view of another specimen. Scale line 5 μm. Figure 11. Operculum, diameter 0.88 mm. Figures 12, 13. ***Xenoskenea*** *pellucida,* operculum, Sicily, diameters 0.46 mm and 0.91 mm.



Explanation of Figures 14 to 17

Figures 14–17. ***Noerrevangia fragilis*** gen. et sp. nov., holotype. Figures 14–16. Shell, diameter 1.7 mm. Figure 17. Larval shell diameter 270 μm.

trophic development to lecithotrophic, great changes in the shape of the protoconch are common and we consider this difference of minor importance.

Although seemingly a minor detail, the fact that the penis is lying parallel to the cephalic tentacle may signify an important character. Almost all caenogastropods keep the penis folded backwards, so it lies along the right corner of the pallial cavity. The position may, however, also be a preservation artifact.

Noerrevangia fragilis
Warén & Schander, sp. nov.

(Figures 14–25)

Type material: Holotype (now badly broken) SMNH 4423.

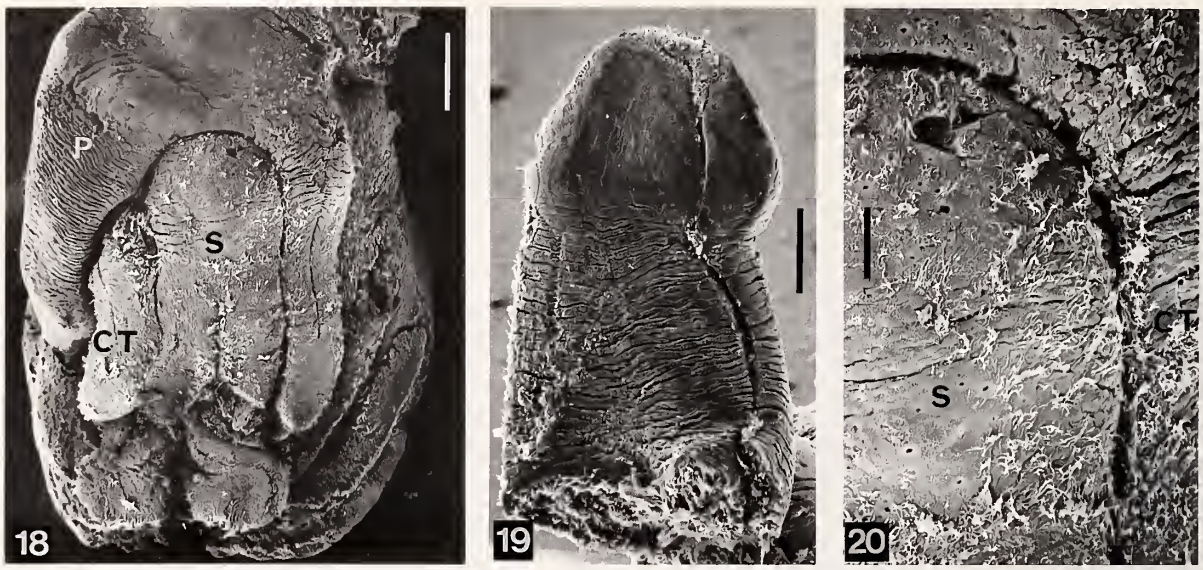
Type locality: The Faeroe Islands, off Thorshavn, 62°04.5′N, 06°42.8′W, 43 m, clay bottom.

Material examined: Known only from the holotype.

Distribution: Known only from the type locality at the Faeroe Islands, in 43 m depth.

Etymology: *Fragilis* (Latin), meaning "fragile."

Description: The shell (Figures 14–16) is small, transparent, vitrinellid-like with a depressed spire, and is very fragile. The larval shell (Figure 17) consists of slightly more than half a whorl with a diameter of 270 μm. It is low and depressed in shape and there are traces of a finely granular sculpture on the initial part, but this area is slightly corroded in the unique specimen. The teleoconch consists of 2.0 whorls of a rounded cross section, slightly



Explanation of Figures 18 to 20

Figures 18–20. ***Noerrevangia fragilis*** gen. et sp. nov., holotype, critical point dried. Figure 18. Contracted head-foot, anterior view. Scale line 100 μm. Figure 19. Penis, ventral view, showing the seminal furrow. Scale line 50 μm. Figure 20. Snout and cephalic tentacle, surface structure. Scale line 25 μm. Key: CT, cephalic tentacle; P, penis; S, snout.

indented by the preceding whorl. The sculpture consists of rather indistinct and slightly flexuous incremental lines. The suture is distinct but not depressed since the outer lip makes a distinct adapical deviation from its circular shape, evening out the transition to the preceding whorl. The aperture is distinctly prosocline and the outer lip slightly sinuated just below the suture. The umbilicus is broad and deep and penetrates the shell to the protoconch.

Dimensions: Diameter 1.7 mm.

Operculum: Round, stiff, colorless, multispiral and smooth, with central nucleus.

Radula (Figures 21–25): Formula 2·2·1·2·2. Central tooth with a sturdy, pointed, and serrated cutting edge and winglike basal supporting ridges. The first lateral tooth is very broad and has two cutting plates, one rounded and more central and one more pointed at the midpoint of the tooth. Lateral to this cutting plate the tooth has a winglike lateral protrusion. The second lateral tooth is very broad and has a rounded, serrated cutting plate occupying the inner one-third of the apical margin. The two marginal teeth are oarlike, long, slender, and serrated along the apical one-third, where they have a thin web along the edge.

Soft parts (Figures 18–20): The foot is anteriorly deeply divided and the corners are drawn out laterally. The propodium is narrow and inconspicuous. Posteriorly the foot does not taper regularly to a point, but probably is deeply notched, as in *Tomura* (but should could not be ascertained because of the contraction of the preserved animal). No epipodial ridges or tentacles were noticed. The snout is long, slender, and bifurcate to half its length. The cephalic tentacles are only sparsely ciliated, are slightly longer than the snout, and lack sensory papillae. Pigmented eyes are lacking. The large penis, attached just behind the right cephalic tentacle, is twice as broad and slightly longer than the tentacle. Its anterior, ventral edge has a deep seminal groove (Figure 19) that lies along the cephalic tentacle. The pallial edge is smooth and simple. Its right corner has a richly ciliated pallial tentacle of half the length of the cephalic tentacles. The ctenidium, which is large and bi-

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Explanation of Figures 21 to 25

Figures 21–25. ***Noerrevangia fragilis*** gen. et sp. nov., radula of the holotype. Numbers indicate the sequence of the teeth, with the central tooth as number 1. Arrows indicate borders between teeth. Figure 21. Oblique view of central and lateral teeth. A marginal tooth (4) is concealing the outer part of the outer lateral tooth. Scale line 10 μm. Figure 22. Oblique view of central and lateral teeth. The point of the more anterior central tooth (1) is concealed by a marginal tooth. Scale line 5 μm. Figure 23. Oblique view of central and lateral teeth. Lateral "wing" of central tooth broken. Scale line 5 μm. Figure 24. Oblique view of lateral teeth. Slightly different angle of Figure 21. Scale line 5 μm. Figure 25. Complete radula, length 215 μm.


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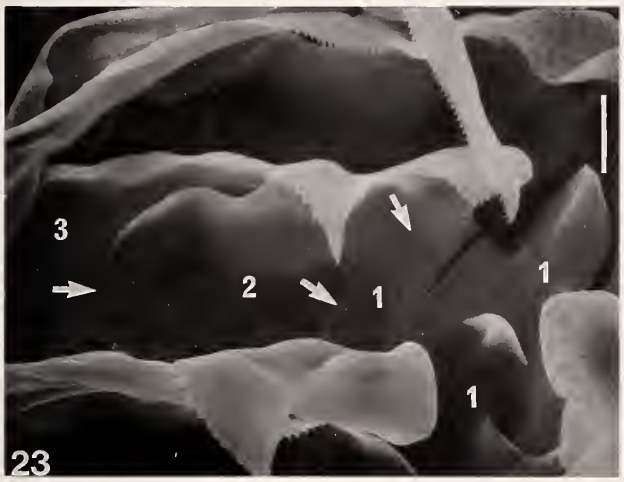
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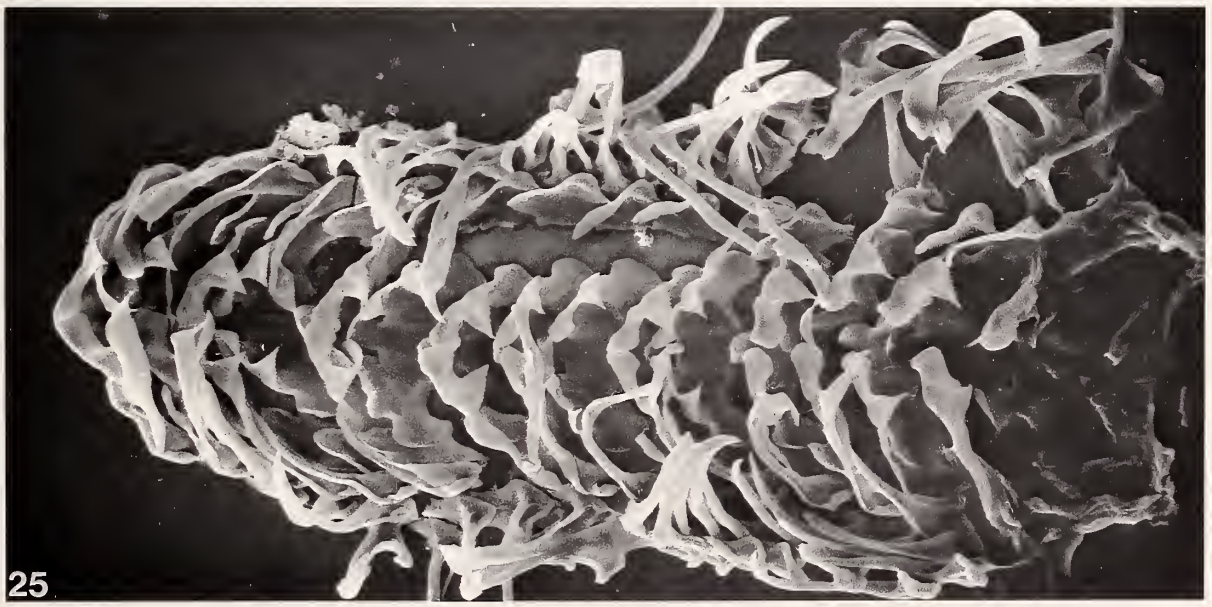
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pectinate, occupies two-thirds of the width of the pallial cavity in the holotype. The digestive gland is richly spotted with brown granules.

Remarks: The shell of this new species is featureless and it would presently be impossible to classify it from conchological characters only. Among European genera it resembles *Skeneopsis* (Skeneopsidae), but species of that genus have a reddish or brownish, more solid shell with a deeper suture, and a protoconch of slightly more than one whorl sculptured with spiral lines and granules. We illustrate the shell, protoconch, and radula of the type species for comparison (Figures 37–41).

The more archaeogastropod-like genus *Akritogyra* Warén, 1992 (systematic position uncertain, provisionally in Skeneidae), resembles *Cornirostra* and ***Noerrevangia***, but the shell has a slightly taller spire and the species have a rhipidoglossate radula with the formula 4–6·2·1·2·4–6 (Warén, 1992). The soft parts of *Akritogyra* are still poorly known.

Family Hyalogryinidae Warén & Bouchet, 1992

Two genera (*Hyalogyra* and *Hyalogyrina,* both described by Marshall, 1988) and four species are so far known to belong to this family (Marshall, 1988; Warén & Bouchet, 1992). These species live on pieces of sunken driftwood or at hydrothermal vents, in fairly deep water, 1000–2000 m.

The species are characterized by:

—a rhipidoglossate radula
—a bipectinate ctenidium
—heavily ciliated areas on the tentacles
—an absence of epipodial tentacles
—the protoconch, if multispiral, is hyperstrophic.

The tentacular arrangement is still uncertain. Anatomical work on *Hyalogyrina* and the new genus described below is being carried out by G. Haszprunar.

Xenoskenea Warén & Gofas, gen. nov.

Type species: *Skenea pellucida* Monterosato, 1874, Mediterranean.

Diagnosis: Heterobranchs with *Vitrinella*-like, small, depressed, perfectly transparent, and almost smooth shell. Protoconch indistinctly hyperstrophic. Teleoconch with 2–3 evenly rounded whorls. Foot large, anteriorly expanded and shallowly bifurcate, posteriorly abruptly drawn out into a narrow, tentacle-like point. Snout large and cylindrical, with small tentacle distally on each side. Right corner of pallial cavity modified to a large pad, covering part of the preceding whorl. Gill bipectinate. Radula rhipidoglossate with formula n·3·1·3·n.

Description: See the description of ***Xenoskenea*** *pellucida*.

Etymology: *Xenos* (Greek), meaning "strange," and *Skenea* (Skeneidae), an archaeogastropod genus with a shell similar to the type species.

Remarks: *Hyalogyra* differs from ***Xenoskenea*** in having a more depressed shell with more shallow suture. *Hyalogyra* also lacks the tentaclelike appendages on the snout and has three tentacles on the head.

Hyalogyrina also differs from ***Xenoskenea*** in lacking the distal appendages of the snout, by having short appendages between the cephalic tentacles or a long appendage laterally to the right cephalic tentacle, and by having a radula with a single row of lateral teeth on each side of the center.

The shell of ***Xenoskenea*** is very similar to that of *Cornirostra,* but has a flexous profile of the outer lip, instead of being straight and radial. Furthermore, *Cornirostra pellucida* has a long, slender right pallial tentacle, whereas ***Xenoskenea*** has a pad covering a part of the early part of the body-whorl, and *Cornirostra* has a bifurcate snout, whereas ***Xenoskenea*** has a cylindrical snout with two tentaclelike appendages. Also the radulae are widely different: ***Xenoskenea*** has a rhipidoglossate radula, whereas that of *Cornirostra* has the formula 1·3·1·3·1.

There are some assumed archaeogastropods which are very similar to ***Xenoskenea***, for example *Akritogyra* Warén, 1992 (provisionally in Skeneidae), but their larval shell has a proportionally larger initial part, which is not sunken in the center (see Warén, 1992:fig. 15A–F). This difference may, however, be due to lecithotrophic development in the species of *Akritogyra.* The external morphology of their soft parts and their anatomy is still largely unknown.

The radula and shell of a new species probably belonging to ***Xenoskenea*** were described from off Luanda (Angola) by Rubio *et al.* (in press). The species was classified in *Hyalogyra* Marshall, but differs from ***Xenoskenea*** *pellucida* only in the shape of the central tooth. We therefore believe that this species belongs to ***Xenoskenea***. The specimens were found on a dead fish from the bottom, and were assumed to be feeding on the carrion.

Xenoskenea *pellucida* was previously tentatively classified in *Skeneopsis* Iredale, 1915 (Skeneopsidae), a genus of littorinoidean affinity (Ponder, 1988). We illustrate the shell, protoconch, and radula of the type species for comparison (Figures 37–41).

Relying on shell morphology, Ponder (1990b:537) suggested that *Skenea pellucida* may belong to the Cornirostridae. This is not supported by the radular morphology.

The second European species of *Skeneopsis, S. sultanorum* Gofas, 1982, remains in *Skeneopsis,* based on observations of living animals (Gofas, unpublished data).

Xenoskenea *pellucida* (Monterosato, 1874)

(Figures 12, 13, 26–36)

Skenea pellucida Aradas & Benoit, 1874:159 (nom. nud.).
Skenea pellucida Monterosato, 1874:263.
Skenea helicina Jeffreys MS, Monterosato, 1874:263 (introduced in synonymy).
Skenea pellucidoides Nordsieck, 1982:46.
Skeneopsis pellucida: Gofas, 1982:232, fig. 8.
Skeneopsis? pellucida: Ponder, 1990b:537.

Explanation of Figures 26 to 30

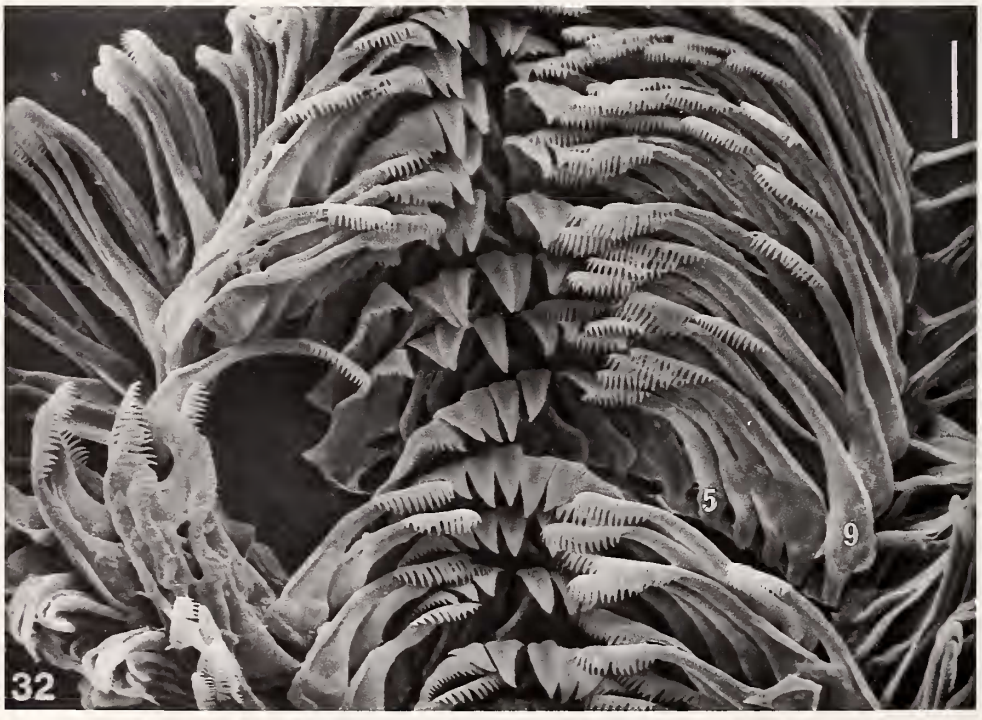
Figures 26–30. ***Xenoskenea*** *pellucida,* Tunisia, Bou Grara Sea. Figure 26. Basal view, diameter 1.56 mm. Figure 27. Apical view of adult specimen, diameter 1.59 mm. Figure 28. Apical view of young specimen, diameter 1.03 mm. Figure 29. Front view, adult specimen, diameter 1.64 mm. Figure 30. Larval shell, diameter 245 μm.

Type materials: *Skenea pellucida,* lectotype (GOFAS, 1982) and 5 paralectotypes in MNHN. *Skenea pellucidoides,* holotype and 1 paratype, Baleares, Ibiza, 50 m and 2 paratypes, Tunisia, Sfax, in Senckenbergisches Museum und Forschungsinstitut, Frankfurt a.M.

Type localities: *Skenea pellucida,* Sicily, Palermo; *S. pellucidoides,* Baleares, Ibiza, 50 m.

Material examined: PORTUGAL, Algarve: Sagres harbor, 9–15 m, rocks with ooze, 4 shells (MNHN); Sagres, Ponta dos Caminhos, 23–33 m, 1 shell (MNHN); Sagres, Bay de Baleeira, 12–17 m, 1 shell (MNHN); Chenal d'Olhao, 3–7 m, in mud covered with *Zostera,* about 20 specimens (SMNH).

(Morocco) CEUTA: El Pineo, 35°52.6'N, 05°19.7'W, 9–10 m, 1 shell (MNHN).



Explanation of Figures 31 and 32

Figures 31, 32. Radula of ***Xenoskenea*** *pellucida*, Brucoli, Sicily. Figure 31. Detail of lateral and central teeth. Scale line 5 μm. Figure 32. Overview, scale line 10 μm.

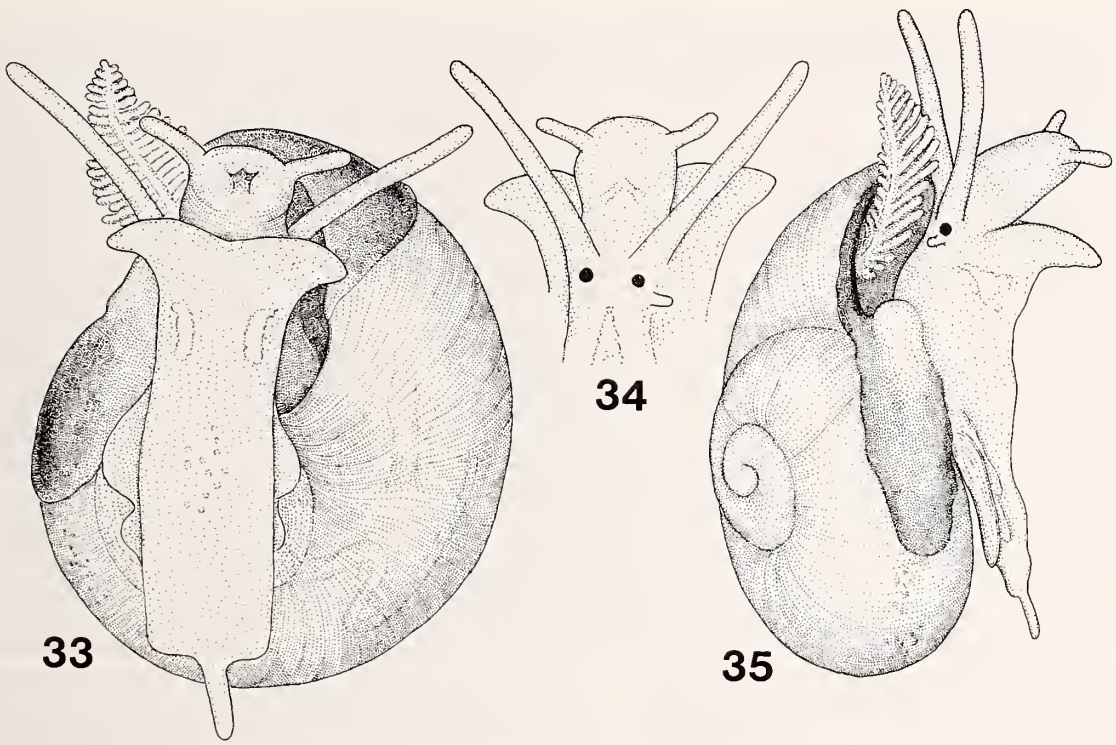
Morocco: Near Oued er Rmel, 35°53.3′N, 05°30.2′W, 13 shells (MNHN).

Algeria: Algiers, coll. Jeffreys, 1 shell (USNM 145049).

Tunisia: Djerba, Borj Jillij, 0–8 m, among *Posidonia*, 2 shells (MNHN); Canal d'Ajim, 10–32 m, 5 shells (SMNH); Bou Grara Sea, littoral, 13 shells (MNHN).

Italy: Gulf of Naples, coll. Jeffreys, 2 shells (USNM 185037); Sicily, no further details, 7 shells (SMNH); Sicily, Trapani, from Monterosato, 4 shells (BMNH); Sicily, Magnisi, Palermo, coll. Jeffreys, 4 shells (USNM 185036); Sicily, S of Catania, Brucoli, *Posidonia* beds, 2 specimens (MNHN); Sicily, no further details, 6 + 10 shells, coll. Jeffreys (USNM 185035 and 202425).

France: Corsica, Baie de Calvi, algal washing, 10–40 m, 1 shell (SMNH).



Explanation of Figures 33 to 35

Figures 33–35. ***Xenoskenea*** *pellucida,* Portugal, Algarve, Ria de Olhâo, Zostera bed, 3 m. Diameter of shell 1.7 mm.

GREECE: Pàtrai lagunar area, 2 shells, *leg.* Nofroni (MNHN).

Distribution: Western and central Mediterranean, to southern Portugal, ca. 0–25 m, on muddy algal bottoms.

Redescription: The shell (Figures 26–29) is *Valvata*-like, small, fragile, completely transparent, smooth except for some growth lines. The larval shell (Figure 30) consists of about 0.75 whorl of rapidly increasing diameter, and its maximum diameter is 250 μm. Its initial part is comparatively small and indistinctly hyperstrophic. The teleoconch consists of up to 2.3 whorls of almost circular cross section, sculptured by sharp, basally flexuous incremental lines. The suture is deep. The area in contact with the preceding whorl occupies 20–30° of the cross section of the whorl and makes a slight dent in the circular shape of the peristome. The umbilicus is deep and wide, and permits examination of the protoconch.

Dimensions: Maximum diameter 2.0 mm.

Radula (Figures 31, 32): The radula is rhipidoglossate with the formula n·3·1·3·n. The central tooth has diverging lateral supports and a slender, triangular cutting surface. The first lateral tooth is similar to the central but has a single lateral support and its inner side fits into a groove between the supporting ridge and "back" of the central tooth. The second lateral tooth is similar to the first one. The third lateral tooth is much broader and the outer part of its cutting edge is serrated. The marginals are at least 10 in number, tall and slender, distally obliquely truncated, and deeply serrated.

Operculum (Figures 12, 13): Thin, colorless, and multispiral with central nucleus.

Soft parts (Figures 33–36): The foot is large and thin, anteriorly expanded and shallowly bifurcate. The sides are parallel, except the anterior and posterior extremities. Pos-

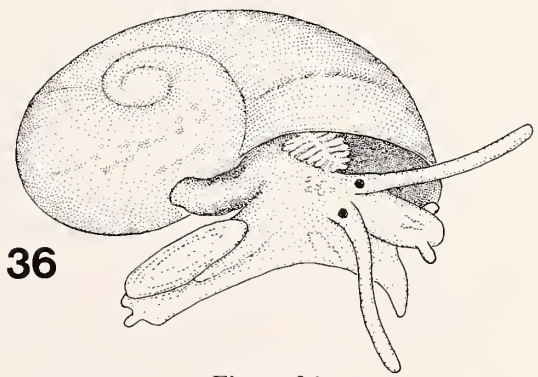
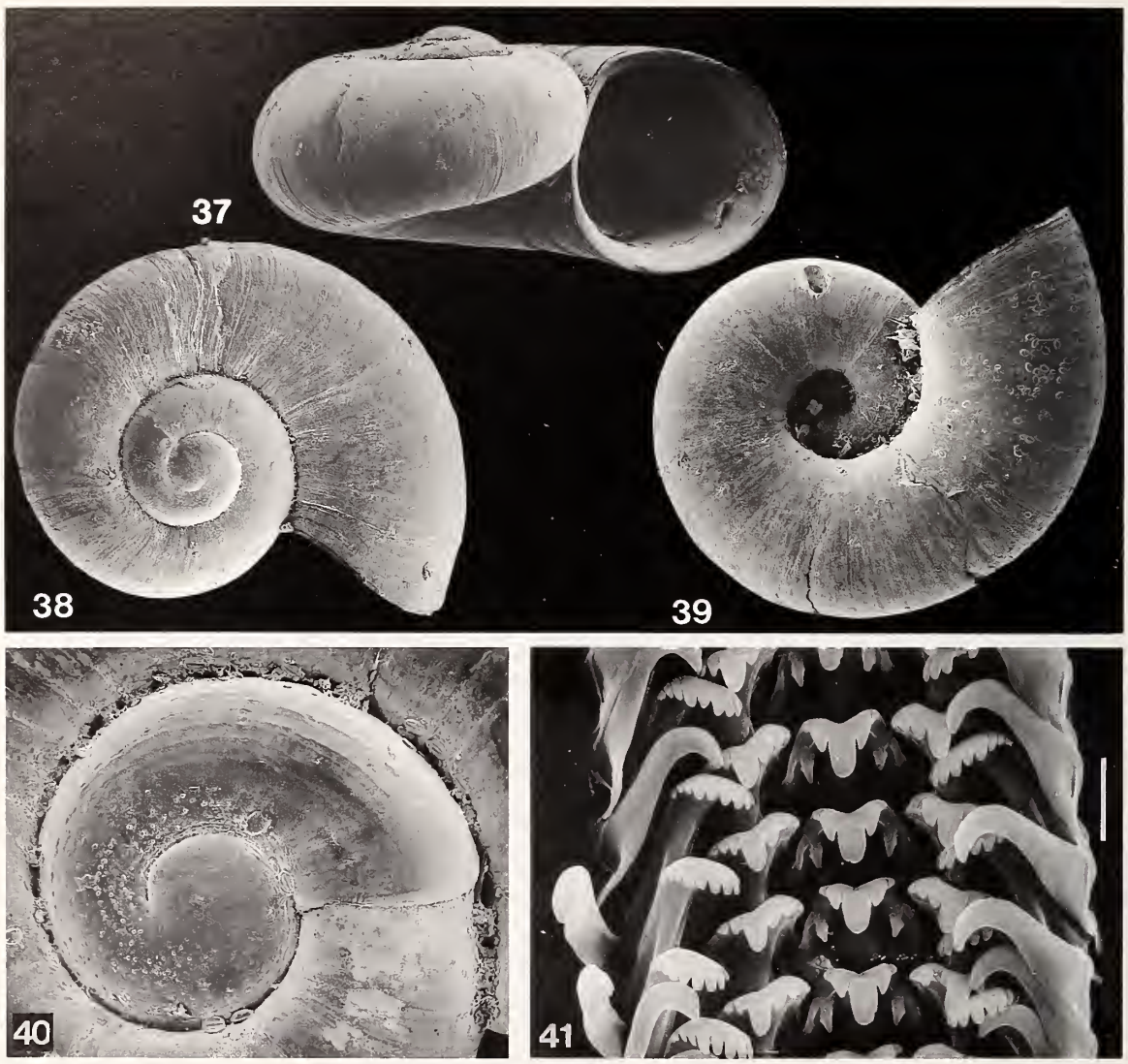


Figure 36

Xenoskenea *pellucida,* young specimen, Sicily, Brucoli, Posidonia bed, 3 m depth. Diameter of shell 1.1 mm.



Explanation of Figures 37 to 41

Figures 37–41. *Skeneopsis planorbis*. Figures 37–39. Shells. Ceuta, Anse Sarchal, intertidal. Diameters 1.3, 1.2, and 1.2 mm. Figure 40. Larval shell. Corsica, Calvi, Punta Revellata, intertidal. Diameter 290 μm. Figure 41. Radula. Norway, Finmark, intertidal. Scale line 10 μm.

teriorly it is abruptly drawn out into a narrow tentacle. The propodium is not externally differentiated. Just behind the corners of the foot, the propodium contains an opaque, yellowish mass of cells close to each side, and centrally there is a group of whitish, superficial spots consisting of glandular cells. The metapodium forms a bilobed skin fold between the operculum and the foot. The snout is large and cylindrical, apically truncated with a centrally situated mouth and a short, cylindrical tentacle on each side. The buccal mass and radula are visible through the transparent snout. The tentacles are long and slender, slightly tapering and lack sensory papillae. The black eyes are embedded in the center of the bases of the tentacles. The penis is small, situated just behind and slightly lateral to the right eye. The pallial margin is simple, dark gray to black, and reflected over the edge of the peristome, especially at the left corner of the aperture. The right corner of the pallial cavity is modified to a large gray, black, or dark brown pad, covering a part of the preceding whorl. The edge of the mantle and the apertural pads are superficially dark gray; the upper part of the snout and the tentacles are only slightly tinged with the same color. The gill is bipectinate with more than 20 pairs of leaflets. It is attached basally, and protrudes from the pallial cavity when the animal is crawling. In live specimens the foodstring could be observed in the upper part of the intestine, rotating clockwise.

Remarks: ***Xenoskenea*** *pellucida* appears to be a rare species, judging from the literature, but this is probably a

collecting bias because it lives on shallow, muddy seagrass- and algal bottoms, which are only rarely examined for this small size range of gastropods.

The shell of ***Xenoskenea*** *pellucida* is just as featureless as the soft parts are characteristic, but there are no species known in shallow Mediterranean waters with which it is likely to be confused.

CARROZZA (1976:fig. 7) used the name *Skenea pellucida* for an unusually smooth specimen of *Skeneopsis planorbis* (Fabricius, 1780).

Xylodiscula boucheti Warén, 1992 (Xylodisculidae, Heterobranchia) is superficially similar but has a flatter spire and broader umbilicus, and lives in deeper water. It has a very different radula with no central tooth.

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LITERATURE CITED

ARADAS, A. & L. BENOIT. 1874 (1872–1876). Conchigliologia vivente marina della Sicilia. Atti dell'Accademia Gioenia di Scienze Naturali, Ser. 3, 4:1–321.

BANDEL, K. 1991. Gastropods from brackish and fresh water of the Jurassic-Cretaceous transition (a systematic reevaluation). Berliner geowissenschaftliche Abhandlungen (A)134: 9–55.

CARROZZA, F. 1976. Microdoride di malacologia mediterranea. (Contributo secundo.) Conchiglie 12:163–169.

FEKIH, M. & L. GOUGEROT. 1977. Liste commentée des gastéropodes testacés marins recueillis dans les dépôts littoraux actuels du Golfe de Tunisia. Bulletin de l'Institut Oceanographique et de Pêche, Salamboo 3:165–232.

GHISOTTI, F. 1984. Problemi di classificazione di "Cyclostrematidae" sensu Jeffreys e gruppi affini per morfologia conchiliare. Lavori della Societa Malacologia Italiana 21:59–66.

GOFAS, S. 1982. Révision des *Skeneopsis* (Gastropoda, Rissoacea) européennes et Nord-Africaines avec description d'une espéce nouvelle. Bollettino Malacologico 18:225–234.

GRANATA, J. GRILLO. 1877a. Contribuzione pella fauna dei molluschi del Mediterraneo.—Il Barth 1877:143–147. [According to information from the National Library of Malta the publication of "Il Barth" was interrupted after this issue, which was dated "8th of November, 1877."]

GRANATA, J. GRILLO. 1877b. Description de quelques espèces nouvelles ou peu connues. S. Marchese, Naples, 15 pp. [Introduction dated August 1877, but Granata talks about his papers in "Il Barth" as being published, so we assume this date to be erroneous.]

HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. Journal of Molluscan Studies 54:367–441.

HEALY, J. M. 1990. Spermatozoa and spermiogenesis of *Cornirostra, Valvata* and *Orbitestella* (Gastropoda, Heterobranchia) with a discussion of valvatoidean sperm morphology. Journal of Molluscan Studies 56:557–566.

MARSHALL, B. A. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. Journal of Natural History 22:949–1004.

MONTEROSATO, T.A. DI. 1874. Recherches conchyliologiques effectués au Cap San Vito, en Sicile. Journal de Conchyliologie, Paris 22:243–282.

NORDSIECK, F. 1982. Die Europäischen Meeres-Gehäuseschnecken. 2nd ed. G. Fischer: Stuttgart. 539 pp.

OLIVERIO, M. 1982. Il genere *Tharsiella* in Mediterraneo (Archaeogastropoda: Skeneidae). Notiziario del CISMA. 4:1–10.

OLIVERIO, M. 1985. Ancora su *Tharsiella depressa* (Granata, 1877). Notiziario del CISMA 5:6–8.

OLIVERIO, M. 1988. Distribuzione geografica di (?)*Tharsiella depressa* (Granata, 1877). (Archaeogastropoda: Skeneidae) Notiziario del CISMA 11:27–29.

PILSBRY, H. A. & T. L. MCGINTY. 1945. Cyclostrematidae and Vitrinellidae of Florida—1. Nautilis 59:1–13.

PILSBRY, H. A. & T. L. MCGINTY. 1946. Cyclostrematidae and Vitrinellidae of Florida—4. Nautilus 60:12–18.

PONDER, W. F. 1986. Glacidorbidae (Glacidorbacea: Basommatophora), a new family and superfamily of operculate freshwater gastropods. Zoological Journal of the Linnean Society 87:53–83.

PONDER, W. F. 1988. The truncatelloidean (=rissoacean) radiation—a preliminary phylogeny. Malacological Review, Supplement 4:129–164.

PONDER, W. F. 1990a. The anatomy and relationships of the Orbitestellidae (Gastropoda: Heterobranchia). Journal of Molluscan Studies 56:515–532.

PONDER, W. F. 1990b. The anatomy and relationships of a marine valvatoidean (Gastropoda: Heterobranchia). Journal of Molluscan Studies 56:533–555.

PONDER, W. F. 1991. Marine valvatoidean gastropods—implications for early heterobranch phylogeny. Journal of Molluscan Studies 57:21–32.

PONDER, W. F. & A. WARÉN. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family group names and higher taxa. Malacological Review, Supplement 4:288–326.

RUBIO, F., E. ROLAN & F. FERNANDES. In press. Nueva especie de *Hyalogyra* (Archaeogastropoda: Skeneidae) procedente de la costa occidental Africana. Bollettino Malacologico.

SABELLI, B., R. GIANNUZZI-SAVELLI & D. BEDULLI. 1990. Annotated check-list of Mediterranean marine mollusks. 1. Edizione Libreria Naturalistica Bolognese. 348 pp.

WARÉN, A. 1991. New and little known Mollusca from Iceland and Scandinavia. Sarsia 76:53–124.

WARÉN, A. 1992. New and little known "skeneimorph" gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. Bollettino Malacologico 27:149–247.

WARÉN, A. & P. BOUCHET. 1992. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. Zoologica Scripta 21.